Title: Drivers of red fox (*Vulpes vulpes*) daily activity: prey availability, human disturbance or habitat structure?

Abbreviated title: Drivers of red fox activity patterns

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Abstract

Daily activity patterns in mammals depend on food availability, reproductive stage, habitat selection, intraspecific interactions and predation risk, among other factors. Some mammals exhibit behavioral plasticity in activity patterns, which allows them to adapt to environmental changes. A good example of this can be found in the red fox *Vulpes vulpes*. This species is adapted to living in highly humanized environments, where it is often culled because it may affect human interests (e.g. through the consumption of game species or livestock). We assessed the potential main drivers of the daily activity patterns of the red fox in 12 Iberian Mediterranean areas through the use of camera traps. Among drivers, we considered main prey availability (wild rabbit *Oryctolagus cuniculus*), degree of human disturbance (e.g. distance to human settlements, and intensity of predator control) and habitat structure. Our results revealed a predominantly crepuscular and nocturnal activity of foxes with local variations. Although overall activity of fox increased with rabbit availability, the temporal overlap with prey activity was on average low, because foxes increased activity when rabbits decreased theirs (twilight-night). Red fox activity rhythms seemed to be determined by human presence where human disturbance is high. In addition, diurnal activity decreased in areas with higher levels of human disturbance (closer to human settlements and high predator control intensity) and increased in dense habitats. Our study shows that daily activity patterns of highly adaptable species are determined by several interacting drivers, resulting in complex behavioral patterns. This suggests that further studies should consider different factors simultaneously for a better understanding of daily activity patterns of wildlife in humanized landscapes.

Key words: camera trap, circadian rhythms, human disturbance, fox control, *Oryctolagus cuniculus*. 
Introduction

Daily activity patterns have been defined as adaptive sequences of routines that meet the time structure of the environment, shaped by evolution and fine-tuned to the actual state of the environment (Halle, 2000). In mammals, daily activity is internally regulated by species-specific endogenous clocks (Kronfeld-Schor & Dayan, 2003), but also by external factors such as nutritional requirements (Masi, Cipolletta & Robbins, 2009), temporal habitat selection (Chavez & Gese, 2006), intraguild interactions (Di Bitetti et al., 2010) or predation risk (Lima & Dill, 1990). Additionally, mammals, as well as other animals, show behavioral responses to environmental changes induced by human activities (Tuomainen & Candolin, 2011).

Similarly to other mammals, daily activity patterns in mammalian predators are mainly determined by both innate activity rhythms and prey availability. The latter has been defined as the combination of prey abundance and their accessibility; prey can be abundant but inaccessible to predators when not active or in inaccessible habitats (Ontiveros, Pleguezuelos & Caro, 2005). A high level of synchrony between predator and prey activity has thus been reported in some cases (Foster et al., 2013; Monterroso, Alves & Ferreras, 2013). Additionally, daily activity patterns of mammalian predators may be influenced by other external factors like habitat structure or human disturbance. Mammalian predators frequently decrease their activity at daytime in open habitats (Chavez & Gese, 2006), where predator removal is conducted (Kitchen et al., 2000) or where human activities such as hunting or outdoor recreational activities are common (Belotti et al., 2012; Ordiz et al., 2012).

We chose the red fox *Vulpes vulpes* as a model to study the flexibility of mammalian predator daily activity patterns due to its high ecological plasticity. The red fox is the most widely distributed mammalian carnivore of the world and it is found in many different habitats, where it can be abundant and feeds on a large variety of foods (Sillero-Zubiri et al., 2004; Díaz-Ruiz et al., 2013). Although the species is a generalist predator, in certain regions such as central-southern Spain, European wild rabbits *Oryctolagus cuniculus* are the fox main prey when abundant (Delibes-Mateos et al. 2008; Díaz-Ruiz et al., 2013). Red foxes have adapted to living in highly human-dominated landscapes, where they take advantage of human subsidiary resources (Bino et al., 2010). On the other hand, they are often persecuted by humans because they feed on game species and
livestock (Sillero-Zubiri et al., 2004). In areas where predator control is carried out more intensively foxes are exposed to a higher ‘risk of predation’ by humans (Reynolds & Tapper, 1996). Thus, fox control could cause stronger fox behavioral responses to human presence in these areas: when hunting constitutes an important source of mortality, human presence itself may create a ‘landscape of fear’ and thereby provoke strong behavioral responses (Martin et al., 2010; Ordiz et al., 2012).

Daily rhythms of activity are among the least studied aspects of the ecology and biology of red foxes. Different studies have shown that red foxes are mainly nocturnal-crepuscular, a pattern that can be explained by factors such as season, habitat structure, prey and human activities (Blanco, 1986; Cavallini & Lovari, 1994; Baker et al., 2007; Monterroso, Alves & Ferreras, 2013; Villar et al., 2013). Notwithstanding, to our knowledge no study has examined the simultaneous influence of ecological (e.g. habitat and prey availability) and human-related factors on red fox activity.

We evaluated the plasticity of red fox daily activity in environments with varying levels of prey availability, habitat structure and human disturbance (e.g. fox control and distance to human settlements) in Mediterranean areas of central Spain, where fox control is a widespread game management tool (Delibes-Mateos et al., 2013; Díaz-Ruiz & Ferreras, 2013). According to previous studies on mammal predator activity we expected that foxes would adapt their activity pattern to that of their preferred prey at least where this is highly available, but that this behavioral pattern could be disrupted by other factors, such as habitat composition or human disturbance. To assess this, we first tested whether the daily activity patterns of the red fox were related to the daily activity of its preferred prey (European wild rabbit) in central Spain (Delibes-Mateos et al. 2008). Secondly, we tested the relationships between the daily activity of red foxes and prey availability, human disturbance and habitat structure simultaneously.

**Material and Methods**

**Study area**

The study was conducted in 12 localities within central Spain (Fig. 1), with Mediterranean-continental climate (Rivas-Martínez, Penas & Diaz, 2004). The landscape was heterogeneous and dominated by cereal croplands and permanent crops such as olive groves and vineyards and natural pastures, mixed with Mediterranean scrubland (mainly
Cistus spp. and holm oak Quercus ilex forests). Other less abundant habitats included riparian habitats, ‘dehesas’ (pastureland with savannah-like open tree layer, mainly dominated by Mediterranean evergreen oaks) and tree plantations (Pinus spp., Eucalyptus spp. and Populus spp.). Villages and scattered dwellings were interspersed in the landscape. Surface and habitat composition varied among localities (see Table 1 for a detailed description).

Agriculture and livestock were the main economic activities in all localities, which were hunting estates too, with the exception of two protected areas where hunting was not allowed (numbers 5 and 11 in Fig. 1). Hunting estates were managed to improve small game populations, mainly by the provision of supplementary food and water, and predator control. Direct shooting and live trapping with cage traps and neck snares are the methods most used for legal fox culling (Delibes-Mateos et al., 2013, Díaz-Ruiz & Ferreras, 2013). In central Spain, there is a high variation in the use of these management measures among hunting estates (Arroyo et al., 2012). In addition, estates usually employ diverse management tools simultaneously and their intensity of use is generally correlated; more intensively managed estates employ more game keepers per km², and have higher hunting pressure (e.g. more hunting days per year) and larger bags (Arroyo et al., 2012). In our study the intensity of fox control also varied largely among hunting estates (Table 1), thus reflecting differences in general game management intensity.

Camera trap surveys

Camera trap surveys were carried out between 2010 and 2013. One sampling survey was developed in each study area between mid-May and mid-August (Table 1) outside the regular hunting season. We used two similar models of infrared-triggered digital cameras: Leaf River IR5 (LeafRiver OutDoor Products, USA) were used only in 2010 surveys (35 cameras), and HCO ScoutGuard (HCO OutDoor Products, USA) in the remaining surveys (179 cameras). Cameras were uniformly spaced in each locality following a grid-sampling scheme according to field features; the average distance between neighbouring cameras was ~1.2 km, boosting independence between them (Monterroso, Alves & Ferreras, 2013; 2014). Between 14 and 20 camera traps were deployed in each study locality, proportionally to locality surface (Table 1). Cameras were mounted on trees approximately 0.5m off the ground and set to record time and date when triggered. Cameras operated 24 h a day for an average period of 28.4 ± 0.4 days (mean ± SE). We
programmed cameras with the minimum time delay between consecutive photos to ensure species identification of each event.

In order to increase the detection probability of red fox, we set the sensitivity of the infrared sensor at the highest level, and used a combination of Valerian scent and Iberian lynx *Lynx pardinus* urine, which is an effective attractant for the red fox (Monterroso, Alves & Ferreras, 2011). Lures were put in two independent perforated plastic vials (3-4 ml) secured to a metal rod, set at 2-3 m from each camera trap, and replenished every two weeks. Consecutive images of the same species within 30 min interval were considered as the same event and those separated by a longer interval as independent events (O’Brien, Kinniard & Wibisono 2003; Davis, Kelly & Stauffer, 2011). To assess the ability of camera-trapping to detect foxes and rabbits we estimated weekly detection probability conditioned to their presence in our study area using single season-species occupancy models (see MacKenzie et al. 2006). Models were built taking into account a habitat covariate (i.e. open or dense, a description of how habitats were classified in these two categories is provided below) that may affect both species detection and occupancy probabilities (MacKenzie et al. 2006).

In an independent study, we tested whether rabbit detection in the cameras was affected by the use of lures. We gathered data during field trials performed in 2013 with the same methodology (n=37 cameras during ~one month) in a near-by area with similar landscape features as in our study areas (i.e. Mediterranean habitats; Monfragüe National Park). Single season-species occupancy models showed that the probability of weekly rabbit detection conditioned to its presence did not change significantly between lured cameras (average detectability ± SE: 0.174±0.105) and non-lured ones (0.03±0.078) (author’s unpublished data), so the use of these scent attractants does not reduce rabbit detectability.

**Relationship between fox and rabbit activity patterns**

We studied the activity patterns of red foxes and rabbits to estimate the probability of both species concurring in a time period. Probability density functions of activity for both species were estimated non-parametrically for each locality from their detection records using kernel density estimates (Ridout & Linkie, 2009). Density functions were only estimated for species in localities with >10 records. We also estimated for each locality the coefficient of overlap $\Delta_1$ for small sample sizes (Ridout & Linkie 2009, Linkie & Ridout 2011) between both species. $\Delta_1$ ranges from 0 (no overlap) to 1 (complete
The precision of this estimator was obtained through confidence intervals as percentiles from 500 bootstrap samples (Linkie & Ridout, 2011). These analyses were performed in R 3.0.1 (R Core Development Team 2013), using an adaptation of the scripts developed by Linkie & Ridout (2011) (http://www.kent.ac.uk/ims/personal/msr/overlap.html).

**Relationship between fox activity, rabbit availability, human disturbance and habitat structure**

Records of red fox activity were assigned to one of three time periods defined according to light levels: i) twilight (one hour prior to sunrise and one hour after sunset, as a semi-darkness period; Mills, 2008); ii) diurnal; and iii) nocturnal periods, taking into account the time of sunset and sunrise in each study site during the sampling period.

We calculated a rabbit availability index for each camera station as the number of independent detections (regardless of time period) of rabbits per 100 trap days (Monterroso, Alves & Ferreras, 2014).

Distance to human settlement was used as a proxy of human disturbance (Ordeñana et al., 2010). We calculated the distance (in kilometres) to the nearest human settlement from each camera using a Geographic Information System (QGIS 1.8.0; QGIS Development Team 2013).

Fox control intensity was gathered through face-to-face interviews with game managers of each hunting estate, conducted in February before field sampling. We asked managers about the number of foxes removed in the previous hunting season (Table 1). We estimated intensity of fox control as the number of foxes removed per km² and year (fox·year⁻¹·km⁻²). As explained above, we used this variable as another index of human disturbance because high levels of predator extraction are generally associated with more game keepers and more intensive management activities (Arroyo et al., 2012).

We grouped habitat types in: dense (including scrubland, forests and riparian habitats) and open habitats (including ‘dehesas’, pasturelands and croplands). Habitat types surrounding each camera trap were identified from CORINE land-cover 2006 and updated satellite orthophotos (Instituto Geográfico Nacional, <http://www.ign.es/>) and checked during fieldwork. Using QGIS 1.8.0, we calculated the percentage of each habitat type (i.e. open versus dense) within a buffer of 200 m radius around each camera trap.
Either open or dense habitat was assigned to each camera trap according to the prevailing category (>50%) within the buffer. Overall, 124 cameras were assigned to open habitat and 90 to dense habitat.

Generalized Linear Mixed Models (GLMM) were employed to assess red fox activity as a function of time period (day, twilight and night), rabbit availability, human disturbance (fox control intensity and distance to human settlement) and habitat type. The response variable was the number of independent red fox detections for each camera in a given time period. It was fitted to a Poisson distribution through a log link function. We included as an offset in the models the trapping effort in each camera for each period and locality, calculated as No. camera-days × period duration in hours, to standardize activity measures in each period per time unit. Camera trap identity was included as a random effect nested within study locality, to account for the non-independence of observations according to these factors. Fixed explanatory effects included: time period and habitat as categorical variables; distance to human settlement, intensity of fox control and overall rabbit availability as continuous variables; and all two-way interactions between time period and other variables. Analyses were carried out with R 3.0.1 with lme4 package (Bates & Maechler, 2010). We compared all possible combinations of these independent effects, as all of those models were biologically plausible, by using the dredge function (package MuMIn; Bartoń, 2012). We selected the models with delta ΔAIC<2, and if no single model accounted for >90% of the total model weights we calculated model-averaged parameter estimates for the variables included in those models (Burnham & Anderson, 2002). We assessed whether models were affected by overdispersion, accepting dispersion parameter levels between 0.5 and 1.5 (Zuur et al., 2009). We also checked for potential collinearity and redundancy of the explanatory variables by analysing the Variable Inflation Factor (VIF). All the predictor variables had VIF <1.26, so they were considered not collinear nor redundant and included in the analysis (Belsley, Kuh & Welsch, 1980).

**Results**

*Red fox daily activity patterns and overlap with rabbit activity*

During a total effort of 6128 trap-days (mean ± SE: 511±27 trapping days·locality⁻¹; Table 1) (all means are presented ± SE), we obtained 610 independent detections of red foxes (51±14 detections·locality⁻¹) and 1190 of rabbits (99±37 detections·locality⁻¹; Table 2).
Mean weekly detection probability was overall similar for both species (red fox: 0.35±0.07; rabbit: 0.33±0.08), but varied among study localities (Table 2).

Red foxes were detected in all localities (Table 2). Fox activity density functions varied slightly among localities but, as a rule, two major activity peaks occurred, one after sunset and another before sunrise (Fig. 2a).

Rabbits were detected in most localities (Table 2). Rabbit activity density functions were similar among localities, revealing a strong bimodal pattern, with a major activity peak occurring after sunrise and throughout the morning and a second peak before sunset (Fig. 2b).

The coefficient of activity overlap between red fox and rabbit was estimated in nine localities with enough detections of both species (Table 2), and varied widely among them, ranging from 0.24 to 0.60 (mean=0.40 ± 0.04; Table 2 and Fig. 3). Activity overlap in a given locality was not correlated with mean rabbit availability in that locality (Pearson’s correlation= − 0.45, p=0.2).

Rabbit availability, human disturbance and habitat structure as factors explaining red fox activity patterns

Five of the evaluated models showed ΔAICc <2, involving a total weight of 0.70 (Table 3). None of these models were affected by overdispersion (dispersion parameter levels: 0.67-0.69). All these models included all the fixed variables, except fox control, which was not included in two of the selected models (Table 3). Interactions between time period and the remaining fixed variables were also included in the selected models (Table 3). The most important variables explaining fox activity were time period, rabbit availability, distance to human settlement and habitat type, and the interactions between time period and both rabbit availability and habitat type (Table 4). Fox control and other interactions between variables contributed less to explain the variability in daily activity of foxes (relative importance <0.6; Table 4).

Model-averaged parameter estimates revealed that red fox activity was in general lowest during daytime, and increased with rabbit availability except during daytime (Table 4; Fig. 4a). Daytime activity of red foxes increased in dense habitats (Day*Dense habitat interaction, Table 4, Fig. 4). Overall red fox activity increased with increasing distance to human settlements (Table 4; Fig. 4b), although that trend was less marked during daytime.
Overall fox activity did not change strongly with fox control, but diurnal activity decreased where fox control was more intense (Day*Fox control interaction, Table 4; Fig. 4c).

**Discussion**

Our results indicate that the red fox is mainly crepuscular and nocturnal in our study areas (Fig. 2a and Table 4). This is in agreement with previous studies across red fox worldwide distribution (Blanco 1986; Sunquist, 1989; Phillips & Catling, 1991; Cavallini & Lovari, 1994) and supports that the red fox is ‘facultative nocturnal’ (Monterroso, Alves & Ferreras, 2014).

Unlike foxes, rabbits presented two main activity peaks in the diurnal time period in our study areas (Fig. 2b). This means that the mean activity overlap between red fox and rabbit (0.40) was low compared with that described for other mammalian predator-prey examples (0.60: Foster et al., 2013; Monterroso, Alves & Ferreras, 2013). Therefore, our results initially disagree with the hypothesis that predators adapt their activity to that of their main prey species (Foster et al., 2013). This partial lack of activity synchrony between predator and its main prey has been previously reported by Arias-Del Razo et al. (2011) and Monterroso, Alves & Ferreras (2013), who interpreted this as an adaptation of prey to reduce predation risk. These low overlaps between rabbit and fox activity patterns may suggest that rabbit activity is not the most important factor explaining variations in red fox activity patterns and suggest the implication of other factors.

In fact, the overlap between rabbit and fox activity was highest during twilight (Table 4 and Fig.3), the time period when rabbits are accessible for foxes. Similarly, our findings show that the overall activity of red foxes increased where rabbits were more available (Table 4 and Fig.4a), reflecting the importance of rabbits in fox diet in central Spain (Delibes-Mateos et al. 2008). However, this increase only occurred during twilight and night time periods, i.e. excluding the period when rabbits were most active and accessible (Table 4 and Fig.3). This suggests that fox activity during daytime is probably constrained by factors unrelated to prey abundance, and also explains the lack of relationship between the coefficient of overlap and rabbit availability at the locality level. Thus, our results could indicate that red foxes do not need a high synchrony with rabbits where the latter are abundant, and/or that prey-predator patterns may be altered by human disturbance, as it has been also suggested for wolves *Canis lupus* and moose *Alces alces* in Scandinavia.
(Eriksen et al., 2009, 2011) or for African lions Panthera leo and wild prey/livestock in Botswana (Valeix et al. 2012).

In our study, red fox activity decreased in areas closer to human settlements, particularly during twilight and night (Table 4 and Fig. 4b), when foxes are overall more active. Several studies have shown that human disturbance caused by activities such as agriculture, stockbreeding or outdoor leisure activities, which frequently take place in our study areas, affect the activity of mammal predators. For example, Matthews et al. (2006) and Belloti et al. (2012) demonstrated that tourist activities altered the activity patterns of black bears Ursus americanus and Eurasian lynxes Lynx lynx, respectively, or road traffic in the case of red foxes (Baker et al. 2007). The effect of human disturbance on predator behavior is especially evident when hunting is an important source of mortality in a given species. In such case, human presence alone may create strong behavioral responses through fear (Martin et al., 2010), which is in accordance with our results.

Culling by humans has been globally identified as an important cause of mortality in the red fox (Sillero-Zubiri et al., 2004). From this point of view, an effect of predator control on the activity pattern of the target species could be expected. For example, in areas where predators are removed, canids decrease their activity, especially during the daytime period (Kitchen, Gese & Schauster, 2000; Rasmussen & Macdonald, 2011; but see Monteverde & Piudo, 2011). In this line, in our study red fox decreased even more its activity during daytime (Table 4 and Fig.4c) in areas with more intense fox control (thus with higher human activity and direct mortality risk). The lack of an overall behavioral response of foxes to predator control intensity, together with the high influence of human presence on fox activity (Table 4 and Fig.4b and c), could indicate that “fear to humans” could be an intrinsic behavior in foxes, accentuated by the historical persecution of this canid by humans in our study area (Vargas, 2002).

The circadian variations in habitat use by hunted species in human-modified landscapes are possibly a response to human presence (Chavez & Gese, 2006; Martin et al., 2010). Therefore, anti-predator behavior in terms of avoidance of human disturbance may explain the observed increase in fox diurnal activity in dense habitats (Table 4), which would be safer for this canid. In agreement with this, several studies have reported that red foxes in rural areas select habitats dominated by dense vegetation during daytime even
Our results show that the red fox presents a high degree of behavioral plasticity adjusting its daily activity rhythms to different ecological scenarios. In this sense, rabbit availability seems to drive fox activity in a scenario of low human disturbance, and foxes actively track rabbits at twilight and night time. However, where foxes are close to urbanized areas or culled, human disturbance may determine the activity of red foxes, which is strongly reduced during daytime, despite the higher accessibility of rabbits then. Our findings show how wildlife adapts to different environmental conditions, including human disturbance, contributing reliable information about an adaptive species such as the red fox. Thus further studies should consider different factors simultaneously for a better understanding of daily activity patterns of wildlife in humanized landscapes.

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Figure 1 Location of the study localities (1-12) in the Iberian Peninsula.

Figure 2 Overall Kernel densities of red fox (a) and rabbit (b) activity in study localities (mean: solid line; range: dashed lines). Vertical dashed lines represent approximate sunrise and sunset times.

Figure 3 Overlap between red fox (dashed line) and rabbit (solid line) activity, determined by camera trapping. The numbers shown in brackets correspond to the study sites ID, as in Fig. 1. Vertical dashed lines represent approximate sunrise and sunset times during the study period in study localities.

Figure 4 Model-averaged relationships between red fox activity (expressed as detections·100 trapping-hour⁻¹) and: a) Rabbit availability (rabbits·100 trapping-day⁻¹), b) Distance to human settlements (km), and c) Fox control (fox·year⁻¹·km⁻²) during the three periods of the daily cycle (day, twilight and night) at two different habitat types (dense and open). For plotting the results, data were back-transformed.
Table 1 Description of study localities (* in the ‘Map ID’ indicates protected areas; the rest were hunting estates). The predominant landscape (agriculture or scrubland) is indicated along with the habitat types present in each area: Oa: open areas, Scr: scrubland, Wc: woody crops, Rip: riparian, Fo: forest, Dh: dehesa. The start and end dates of each survey are shown in the sampling year column. ‘Cameras’ indicate the number of camera traps used in each locality. ‘Effort’ (survey effort) is expressed as camera-days, or the sum of days each camera was active in the field in each locality. Descriptive statistics of independent variables for each study locality are also shown: ‘Rabbit availability’ is expressed as the number of independent detections of rabbits per 100 trap days; ‘Distance’ is the distance in km to the nearest human settlement; ‘Red fox control’ refers to the number of foxes culled per square km and year; ‘Habitat’ represents the number of cameras assigned to open or dense predominant habitat, respectively.

<table>
<thead>
<tr>
<th>Study site (Map ID)</th>
<th>Area (km²)</th>
<th>Landscape (habitat types)</th>
<th>Sampling year (start/end)</th>
<th>Cameras</th>
<th>Effort</th>
<th>Rabbit availability (mean±SE)</th>
<th>Distance (km) (mean±SE)</th>
<th>Red fox control (foxes km⁻² year⁻¹)</th>
<th>Habitat (open/dense)</th>
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<tr>
<td>1 20 Agricultural (Oa, Scr, Rip, Wc)</td>
<td>20</td>
<td>2010 (Jul/Aug)</td>
<td>20</td>
<td>620</td>
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<td>2011 (Jun/Jul)</td>
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<td>417</td>
<td>-</td>
<td>9.21 ± 0.64</td>
</tr>
<tr>
<td>10</td>
<td>9</td>
<td></td>
<td>Agricultural (Oa, Scr, Rip)</td>
<td>2012</td>
<td>May/Jun</td>
<td>14</td>
<td>372</td>
<td>106.07 ± 64.01</td>
<td>5.18 ± 0.71</td>
</tr>
<tr>
<td>11*</td>
<td>26</td>
<td></td>
<td>Scrubland (Oa, Scr, Rip)</td>
<td>2012</td>
<td>May/Jun</td>
<td>20</td>
<td>529</td>
<td>2.23 ± 1.43</td>
<td>8.83 ± 1.40</td>
</tr>
<tr>
<td>12</td>
<td>16</td>
<td></td>
<td>Scrubland (Oa, Scr, Rip, Dh, Fo)</td>
<td>2013</td>
<td>May/Jun</td>
<td>18</td>
<td>463</td>
<td>2.31 ± 2.31</td>
<td>9.30 ± 1.40</td>
</tr>
</tbody>
</table>
Table 2 Number of independent detections of red fox and rabbit and coefficient of overlap ($\Delta_1$) of daily activity patterns of red fox and rabbit in each locality. CI95% is the 95% bootstrap confidence interval. Weekly detection probabilities ($P$) conditioned to presence for both species are also shown (estimated using occupancy models).

<table>
<thead>
<tr>
<th>Study site (Map ID)</th>
<th>Nº Red fox detections</th>
<th>Nº Rabbit detections</th>
<th>$\Delta_1$</th>
<th>CI 95%</th>
<th>$P$ red fox</th>
<th>$P$ rabbit</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>17</td>
<td>48</td>
<td>0.48</td>
<td>(0.33-0.67)</td>
<td>0.10</td>
<td>0.34</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
<td>101</td>
<td>-</td>
<td>-</td>
<td>0.04</td>
<td>0.51</td>
</tr>
<tr>
<td>3</td>
<td>35</td>
<td>343</td>
<td>0.33</td>
<td>(0.31-0.52)</td>
<td>0.39</td>
<td>0.80</td>
</tr>
<tr>
<td>4</td>
<td>77</td>
<td>176</td>
<td>0.43</td>
<td>(0.36-0.56)</td>
<td>0.57</td>
<td>0.63</td>
</tr>
<tr>
<td>5</td>
<td>38</td>
<td>108</td>
<td>0.6</td>
<td>(0.39-0.66)</td>
<td>0.30</td>
<td>0.36</td>
</tr>
<tr>
<td>6</td>
<td>22</td>
<td>18</td>
<td>0.49</td>
<td>(0.36-0.72)</td>
<td>0.14</td>
<td>0.09</td>
</tr>
<tr>
<td>7</td>
<td>17</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>0.21</td>
<td>0.00</td>
</tr>
<tr>
<td>8</td>
<td>39</td>
<td>12</td>
<td>0.46</td>
<td>(0.29-0.63)</td>
<td>0.37</td>
<td>0.19</td>
</tr>
<tr>
<td>9</td>
<td>89</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>0.55</td>
<td>0.00</td>
</tr>
<tr>
<td>10</td>
<td>48</td>
<td>357</td>
<td>0.26</td>
<td>(0.15-0.32)</td>
<td>0.33</td>
<td>0.80</td>
</tr>
<tr>
<td>11</td>
<td>180</td>
<td>16</td>
<td>0.24</td>
<td>(0.25-0.49)</td>
<td>0.84</td>
<td>0.14</td>
</tr>
<tr>
<td>12</td>
<td>44</td>
<td>11</td>
<td>0.35</td>
<td>(0.11-0.56)</td>
<td>0.41</td>
<td>0.08</td>
</tr>
</tbody>
</table>
Table 3 Models explaining red fox activity (number of independent red fox detections for each camera in a given period). We present data for those models with $\Delta$AIC<sub>c</sub>&#x2264;2, as well as the full and null models. Variables are, *Time*: timer period (day, night and twilight), *Hbt*: habitat type (dense or open), *Dst*: distance to human settlement, *Rab*: rabbit availability, *Fc*: fox control. Interactions between variables are represented by *.

<table>
<thead>
<tr>
<th>Model</th>
<th>df</th>
<th>logLik</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>w</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Time+Hbt+Dst+Rab+Time\ast(Hbt+Rab)$</td>
<td>12</td>
<td>-421.74</td>
<td>867.99</td>
<td>0</td>
<td>0.20</td>
</tr>
<tr>
<td>$Time+Hbt+Dst+Rab+Time\ast(Dst+Hbt+Rab)$</td>
<td>14</td>
<td>-419.73</td>
<td>868.13</td>
<td>0.14</td>
<td>0.18</td>
</tr>
<tr>
<td>$Time+Fc+Hbt+Dst+Rab+Time\ast(Fc+Hbt+Dst+Rab)$</td>
<td>17</td>
<td>-416.82</td>
<td>868.63</td>
<td>0.64</td>
<td>0.14</td>
</tr>
<tr>
<td>$Time+Fc+Hbt+Dst+Rab+Time\ast(Hbt+Rab)$</td>
<td>13</td>
<td>-421.43</td>
<td>869.44</td>
<td>1.46</td>
<td>0.09</td>
</tr>
<tr>
<td>$Time+Fc+Hbt+Dst+Rab+Time\ast(Hbt+Dst+Rab)$</td>
<td>15</td>
<td>-419.42</td>
<td>869.61</td>
<td>1.63</td>
<td>0.09</td>
</tr>
<tr>
<td>Full model</td>
<td>18</td>
<td>-416.79</td>
<td>870.70</td>
<td>2.69</td>
<td>0.05</td>
</tr>
<tr>
<td>Null model</td>
<td>3</td>
<td>-604.63</td>
<td>1215.30</td>
<td>347.31</td>
<td>0.00</td>
</tr>
</tbody>
</table>
Table 4 Model averaged coefficients and standard errors of the variables included in the five best models explaining the red fox activity (number of independent red fox detections for each camera in a given period). ‘RI’ is the relative variable importance from model average, ‘Time’ is the time period (day, night or twilight), ‘Distance’ is the distance to human settlement, and ‘Rabbit’ is the availability of rabbits.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>SE</th>
<th>z</th>
<th>RI</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-3.576</td>
<td>0.455</td>
<td>7.860</td>
<td>-</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Time: Twilight</td>
<td>0.031</td>
<td>0.264</td>
<td>0.119</td>
<td>1</td>
<td>0.905</td>
</tr>
<tr>
<td>Time: Day</td>
<td>-1.469</td>
<td>0.347</td>
<td>4.232</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Fox Control</td>
<td>-13.1</td>
<td>19.2</td>
<td>0.686</td>
<td>0.46</td>
<td>0.492</td>
</tr>
<tr>
<td>Habitat: Dense</td>
<td>-0.046</td>
<td>0.253</td>
<td>0.181</td>
<td>1</td>
<td>0.856</td>
</tr>
<tr>
<td>Distance</td>
<td>0.159</td>
<td>0.062</td>
<td>2.736</td>
<td>1</td>
<td>0.009</td>
</tr>
<tr>
<td>Rabbit</td>
<td>0.004</td>
<td>0.001</td>
<td>3.870</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Twilight*Fox Control</td>
<td>3.923</td>
<td>11.06</td>
<td>0.369</td>
<td>0.20</td>
<td>0.712</td>
</tr>
<tr>
<td>Twilight*Dense habitat</td>
<td>0.192</td>
<td>0.237</td>
<td>0.811</td>
<td>1</td>
<td>0.417</td>
</tr>
<tr>
<td>Twilight*Distance</td>
<td>-0.001</td>
<td>0.043</td>
<td>0.036</td>
<td>0.59</td>
<td>0.971</td>
</tr>
<tr>
<td>Twilight*Rabbit</td>
<td>0.001</td>
<td>4.10^{-04}</td>
<td>2.037</td>
<td>1</td>
<td>0.041</td>
</tr>
<tr>
<td>Day*Fox Control</td>
<td>-22.9</td>
<td>11.5</td>
<td>1.979</td>
<td>0.20</td>
<td>0.047</td>
</tr>
<tr>
<td>Day*Dense habitat</td>
<td>0.910</td>
<td>0.223</td>
<td>4.082</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Day*Distance</td>
<td>-0.076</td>
<td>0.037</td>
<td>2.043</td>
<td>0.59</td>
<td>0.041</td>
</tr>
<tr>
<td>Day*Rabbit</td>
<td>-0.002</td>
<td>0.001</td>
<td>2.273</td>
<td>1</td>
<td>0.023</td>
</tr>
</tbody>
</table>
Figure 2
Figure 3

(1) 

(3) 

(4) 

(5) 

(6) 

(8) 

(10) 

(11) 

(12)
Figure 4

(a) Graph showing activity levels at different times of day (Twilight, Night, Day) and weather conditions (dense, open) against rabbit availability.

(b) Graph showing activity levels against distance to human settlement.

(c) Graph showing activity levels against fox control levels.